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Effects of rearing treatment on the behavior of captive whooping cranes (*Grus americana*)

Michael D. Kreger^{a,*}, Inma Estevez^b, Jeff S. Hatfield^c, George F. Gee^c

^aDivision of Scientific Authority, U.S. Fish and Wildlife Service, 4401 N. Fairfax Dr., Room 750, Arlington, VA 22203, USA ^bDepartment of Animal and Avian Sciences, University of Maryland, College Park, MD 20742, USA ^cUSGS Patuxent Wildlife Research Center, Laurel, MD 20708, USA

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Abstract

Small founder populations of whooping cranes are managed to maximize egg production for the purpose of reintroducing young to the wild. This results in an excessive number of hatched chicks that cannot be naturally reared by parents. Hand-rearing techniques have been developed to raise the additional hatches. However, hand rearing may affect the behavior of the birds and their chances of survival later in life. The objectives of this study were to determine the impact of rearing practices on the behavior of whooping crane chicks. The birds were reared under three commonly used rearing techniques: parent reared (PR), hand reared (HR), and hand reared with exercise (HRE). Fifty-six whooping crane chicks were observed by focal animal sampling from hatch to 20 weeks of age. During these observations, occurrences of comfort behavior, aggression, foraging, nonvigilance, sleep, vigilance, and other types of behavior were collected. Data were analyzed using mixed models repeated measures analysis of variance (ANOVA). Behavior was affected by rearing treatment, age, and time of day. PR birds spent more time being vigilant than HR and HRE birds. An inverse correlation was found between percentage of time foraging and vigilant (r = -0.686, P < 0.0001). However, there were no differences in the behavior of birds reared in HR or HRE programs. © 2004 Published by Elsevier B.V.

Keywords: Whooping crane; Grus; Hand rearing; Parent rearing; Foraging; Vigilance

^{*} Corresponding author. Tel.: +1 703 3582489; fax: +1 703 3582276. E-mail address: michael_kreger@fws.gov (M.D. Kreger).

1. Introduction

Endangered species reintroduction programs established to breed, rear, and reintroduce endangered birds such as whooping cranes (*Grus americana*) (Ellis et al., 1992; U.S. Fish and Wildlife Service, 1994), Mississippi sandhill cranes (*Grus canadensis pulla*) (Ellis et al., 2000), and the California condor (*Gymnogyps californianus*) (Wallace, 1994) rely on maximizing production of the individuals in captivity. This is necessary because the programs often begin with a small number of founder individuals or parent stock. Large numbers of captive-reared individuals are needed to fuel the release program as well as to maximize the genetic diversity of the captive population (Hutchins et al., 1995; Ballou and Foose, 1996). Techniques, such as double clutching and artificial insemination, have been developed to maximize egg production (Gee, 1983; Gee and Mirande, 1996). This results in more chicks hatched than can be reared by parents. Therefore, alternative hand-rearing methods must be used.

Also, behavioral and management concerns may preclude chicks from being parent reared. Parents may reproduce but lack parenting skills (Hutchins et al., 1995) and may be inattentive, not provide adequate care, or injure and cannibalize the young. Parent-reared young may require veterinary intervention that prevents them from rejoining the parents (Wellington et al., 1996). In addition, depending on the life history of the species, survival of young is not always favorable under parent rearing. In the wild, whooping cranes usually lay two eggs per clutch, chicks typically hatch asynchronously, and siblicide is common depending on the availability of food resources (Archibald and Lewis, 1996). To compensate for the loss of parental care, hand-rearing techniques have been developed to raise the additional young. Furthermore, whether reared by parents or hand reared, rearing of birds out of their native environment may have a profound effect on their behavior and may impinge on their chances of survival later in life.

There are benefits to the young from parent rearing. In the wild, parents of precocial birds, like cranes, feed the young, teach them how to identify and handle appropriate food items, and spend much of their time protecting the young from predators (Clutton-Brock, 1991; Hutchins et al., 1995). Indeed, common crane (*Grus grus*) parents spend more time scanning and less time foraging and resting than non-parents (Alonso and Alonso, 1993). Depending on the bird species, the chicks may learn predator recognition, nestbuilding skills, offspring rearing, migratory routes, and appropriate vocalizations from parents (Weller and Ward, 1959; Hutchins et al., 1995; Curio, 1998).

Since no human can replicate the entire regimen of behavioral skills that a chick requires to survive, it would seem that parent-reared birds would have an advantage in survival after reintroduction over hand-reared birds. However, captivity may also affect the behavior of the parents or adults that may serve as surrogate parents. Parents may behave differently from their wild counterparts, particularly if they were not reared by wild founder stock (Költringer et al., 1995; Snyder et al., 1996; Curio, 1998). Offspring may learn inappropriate behaviors such as stereotypic pacing, which is more a function of captivity and will not have survival value (Curio, 1993; 1998).

In hand rearing, a variety of husbandry techniques are used to mimic parental behavior and minimize human imprinting (Wallace, 1994; Horwich, 1996; Swengel et al., 1996). Providing exposure to predators, placement of food throughout an enclosure to

encourage foraging behavior, and rearing the young with adult models in view are techniques that expose the young to stimuli that may be encountered in the wild (Kreger et al., 1998). In some instances, such as for Mississippi sandhill cranes (Ellis et al., 2000) and houbara bustards (*Chlamydotis undulata*) (Van Heezik and Seddon, 1998), post-release survival of artificially-reared birds was as good or better than parent-reared birds.

Rearing methods that stimulate behavior, adaptive to challenges faced in the wild, are particularly critical to reintroduction programs. Such behaviors include avoiding predators, acquiring food, interacting socially with conspecifics, locomoting on complex terrain, and orienting and navigating in a complex environment (Kleiman, 1996). Predatory skills of the endangered black-footed ferret (*Mustela nigripes*), for example, were greater in a complex captive environment that encouraged foraging (e.g., cages provided with plastic tunnels, cement blocks, and an additional nest box) than ferrets raised in a standard cage (Vargas and Anderson, 1999). Whether or not this confers survival advantages post release is often difficult to determine due to the individual animal's experience. Each animal may respond differently to factors such as social structure, the presence of humans, and lifestyle changes from husbandry actions (i.e., movement from pen to pen, changes in group composition) (Castro et al., 1998). This may also explain why post-release survival of golden lion tamarins (*Leontopithicus rosalia*) did not differ among groups that received pre-release foraging and locomotion training and those which did not (Castro et al., 1998).

The potential consequences of rearing methods on survival of birds in reintroduction programs have been extensively investigated (see reviews in Hutchins et al., 1995 and Curio, 1998). However, most of the studies describe rearing methods and hypothesize how they may have affected post-release survival (Powell and Cuthbert, 1993; Van Heezik et al., 1999; Ellis et al., 2000). While some avian studies have examined effects of rearing treatments on survival, few have investigated their effects on the behavior of pre-release captive animals (Van Heezik and Seddon, 1998) and even fewer have determined the impact on survival upon release. Previous studies of captive whooping cranes have identified their behavioral repertoire (Ellis et al., 1998, 1991; Watanabe, 1996). However, no study has been conducted to investigate the impact the different rearing practices may have on the behavior of the young whooping cranes for subsequent reintroduction and on their chances of survival. This study is part of a larger project in which we investigated consequences of the three most commonly used practices to captive rear whooping crane chicks within the Whooping Crane Recovery Plan (U.S. Fish and Wildlife Service, 1994) and their impact on survival, once released (Kreger, 2003; Kreger et al., in review, in preparation). Thirty-four of the 56 birds reared in this study were released as part of a nonmigratory flock being established in Florida. Fifty-five percent of the released birds survived their first year (Kreger, 2003; Kreger et al., in preparation). Kreger (2003) and Kreger et al. (in review) describe the behavior of these birds after release. Kreger (2003) and Kreger et al. (in preparation) include a survival analysis and an assessment of the relationship between behavior and survival.

In this paper, we focus on the impact of the three most commonly used rearing treatments (parent reared, hand reared, and hand reared with exercise) on the behavior of whooping cranes until 20 weeks of age. This is the time when managers start quarantine to

prepare the birds for their release into the wild. Within this study, we were particularly interested in determining differences regarding vigilance behavior. These differences can be critical to their chances for survival once the birds are released. Thus, this study provides information that may be used to improve rearing practices to raise captive whooping cranes for reintroduction.

2. Methods

Experimental treatments consisted of hand reared (HR), hand reared with exercise (HRE), and parent reared (PR) birds. All chicks were fed a nutritionally balanced diet of crane starter crumbles from hatch to 20 days and in pellets from 20 to 70 days of age (23.8% protein, 2689 kcal/kg energy). At 70 days of age, a maintenance diet was used (19.4% protein, 2530 kcal/kg energy; Swengel and Carpenter, 1996).

2.1. Hand-reared and hand-reared with exercise treatments

Eggs were removed from the nest, and either moved to a surrogate crane for incubation or placed in an incubator with a dry-bulb temperature of 37.6 °C and a wet-bulb temperature of 30.0 °C (61% relative humidity). The chicks hatched between 28 and 34 days of incubation (mean was 29 days). Once pipping began, the incubator chick was placed in a hatcher at 73% and humidity at 37.2 °C to facilitate hatching. When the chick was dry (4-24 h post-hatch), it was placed in an intensive care unit for early training to eat and drink before being transferred to the indoor portion of an individual pen between two and five days of age. Chicks that pipped under a surrogate adult were removed and placed directly in the individual pen. Each pen consisted of a 2.4 m \times 2.4 m indoor area connected by a door to a 2.4 m × 20.0 m grassy outdoor area. A drinker and gravity feeder were provided in both areas. Adjoining pens were separated by wire mesh and plexiglass that allowed visual contact among chicks. A sub-adult or an adult was placed in an empty pen between two chick pens or in a large pen parallel to the outdoor chick pens within their view, so that it could be used as a model for the chicks. Both HR and HRE chicks were housed in these individual pens until 55-60 days of age (Wellington et al., 1996).

After 55–60 days of age the birds were transferred into large group pens with six to eight young of similar age until they reached at least 140 days of age. Birds hatched in 1998 were observed in outdoor areas (12.19 m \times 30.48 m). In 1999, HR and HRE birds were housed in different outdoor pens (15.24 m \times 30.48 m) due to the unavailability of the pens used the previous year. All pens contained two shelters, one near the pen entrance (1.83 m \times 1.83 m) containing the feeder and the drinker, and a second shelter (1.22 m \times 1.22 m), located in the center of the pen. All pens were made of chain-link fence covered with a mesh ceiling so birds could gain flight experience without escaping. Caretakers selected group members in each pen based on closeness of age and compatibility. With the exception of the use of heat lamps for HR and HRE chicks under two weeks of age, all birds were exposed to natural photoperiods and ambient temperatures of Laurel, Maryland, USA (39°3′N, 76°49′W).

2.2. Animal care and exercise program

Human caretakers, who provided daily care and behavioral training, reared HR and HRE chicks. The caretaker used a taxidermy hand puppet of a crane head and neck to mimic the appearance and movements of an adult whooping crane. The puppet was used to encourage the chick to feed and drink. To minimize imprinting on humans and still function as the surrogate parent, the caretaker wore a costume consisting of a white cotton poncho and hood with a dark fabric screen over the face. The costumes allowed easy inspection of the birds, medical or social intervention if necessary. Non-costumed caretakers were periodically used for aversive conditioning to humans (Horwich, 1996; Swengel et al., 1996; Wellington et al., 1996).

As per standard management practices, starting at about 6 days of age until 25 days, caretakers placed HR and HRE birds in a swimming pool where chicks were allowed to swim for 2–20 min so they could develop strong leg bones and muscles. Additionally, from 26 to 55 days of age, the birds were led by caretakers to a yard with a small shallow marsh to forage and socialize with other chicks. The HRE birds were led on short walks around the rearing pens from one to 25 days. The walks were believed to provide extra stimulation for muscle development and reduce leg problems (Olsen, 1994; O'Malley, 1999). Walking sessions continued until the birds were moved into group pens around 55 days of age. This was the only difference between HR and HRE reared birds.

2.3. Parent-reared birds

Within the PR treatment a single chick was raised by a pair of adult whooping cranes until 140 days. Then chicks were placed in a group pen with six to eight other PR birds as a release cohort for reintroduction. The adult pair may have been the biological parents or surrogate parents.

PR birds were maintained in family groups in outdoor 13.72 m \times 19.81 m pens. Each pen contained two gravity feeders hanging from a shelter, and drinker that provided ad libitum water. One shelter was located near the pen entrance (6 m × 6 m) and the other $(3 \text{ m} \times 3 \text{ m})$ was located in the center of the pen. Only alternate pens were occupied. Because wild whooping cranes are territorial breeders (Allen, 1952), empty pens wrapped with tennis mesh around their periphery provided visual barriers to simulate isolated territories. All pens were constructed of chain-link fence and contained a mesh ceiling. Cranes in these facilities rarely interacted with humans. Caretakers serviced the pen as little as possible and did not wear costumes with the expectation that the birds would respond to humans as an aversive stimulus and, thus, not approach humans upon reintroduction. Unlike HR and HRE birds, PR birds were not exercised by caretakers. The chicks were picked up and examined for the first three to four days. They were observed from a distance when not handled for examination, once every 5 days (day 4-25) and once every 7 days to day 65. Feed and water were placed close to the chick for the first few days, after which, caretakers tried to avoid entering a pen (other than to refill gravity feeders or weigh chicks or treat infections). All birds experienced natural photoperiods and ambient temperatures.

At 140 days, the birds were mixed with other individuals to establish the release cohorts and begin quarantine procedures. These pens were similar to those of the HR and HRE birds.

The rearing methods and management of the cranes were typical husbandry practices at the rearing facility and could not be established or controlled for this study. We recognize that in this study, several variables such as group size, pen size, and age effects are confounding. Group size of the PR birds was three (two adult birds (usually the parents) and the chick) while HR and HRE birds were in groups of six to eight birds (same age) after 55 days. Although confounding makes it difficult to speculate on the contribution of pen size or population density to our results, this is standard husbandry at the U.S. Geological Survey Patuxent Wildlife Research Center and could not be changed for the purposes of this study due to the importance of each crane in the reintroduction program. Thus, our results compare rearing protocols that include confounding of certain pen sizes and population densities.

2.4. Behavioral observations

The first chicks hatched in April of 1998 and 1999. In 1998, there were 13 HR birds, 8 HRE birds, and 8 PR birds. In 1999, there were 13 HR, 7 HRE, and 7 PR birds. Therefore, data were collected on a total of 56 birds. Each bird was individually identified with colored leg bands. There were mortalities (6 HR, 2 HRE), but the birds were observed until they were removed for veterinary treatment, euthanized, or found dead. A Fisher's exact test comparing mortality among rearing treatments was not statistically significant (P = 0.1530).

The behavioral observations took place from hatch to 140 days of age and resulted in 248 h of observations over the 2-year study. Observations on the HR and HRE birds began when the chick was placed in the individual pen (usually 2 to 5 days after hatching). A costumed observer sitting in the service aisle that separated two rows of indoor pens recorded behavior of HR and HRE birds. If the chick crossed into the outdoor area of the pen, the observer could still view the chick from the aisle through the open door separating the indoor and outdoor areas. The costume was the same as that described for the caretaker and therefore it did not appear to disrupt the normal behavior of the birds. Once the chicks were moved to group pens, the costumed observer watched the birds from an empty pen between the occupied pens or from the lawn in front of the pen.

Observations of PR chicks earlier than 21 days of age were opportunistic because they were often concealed by vegetation within the pen. Routine observations began after all eggs had hatched and the youngest chick was 21 days of age. A small one-person dome tent was used as a blind for the data collection of these groups of birds. Because the birds were in enclosed conditions and were visible most of the time regardless of rearing treatment, all observations were used.

Predation by bobcats (*Lynx rufus*) was the highest cause of mortality in birds released in Florida (Nesbitt et al., 2001) and it is suspected that most of the predation occurred between early evening and dawn (Wassmer et al., 1988). For this reason, we were particularly interested in describing the behaviors in captivity that occurred in the early morning and

late afternoon. Therefore, observations were conducted between 05:00 and 08:00 and 15:30 and 18:30 h. This time was before the arrival of the animal care staff in the morning and after their departure in the afternoon, which prevented disruption of the observations. For all rearing treatments, behavioral data were collected using 5-min continuous focal sampling (Crockett, 1996). Each individual was observed for a minimum of six times per two-week age period from hatch to 20 weeks of age. The order of observations was randomized across individuals, but balanced for time of day. A 5-min habituation period was allowed before starting the observations to ensure that the behavior of the birds was not due to the presence of the observer.

Observers recorded data on a standardized form which included the date, bird identification number, pen number, and time of day. The time a behavior was initiated was recorded along with the type of behavior. The behavioral categories defined were broad, but encompassed the crane behaviors described by Ellis et al. (1991).

Four volunteers, University of Maryland graduate students, participated in data collection during the 1998 season and two in the 1999 season. Each sat with the researcher for a week as observations were performed. Although the behavioral reactions of the birds to the presence of two observers versus a single observer were not evaluated, the effects were believed to be minimal since all observers wore costumes identical to those worn by caretakers. At the end of the week, interobserver reliability with the researcher was determined by the Index of Concordance (Martin and Bateson, 1993) and was at least 90%, which is considered to be acceptable (Lehner, 1996, p. 216).

The behavioral repertoire (modified from Ellis et al., 1991) included the following behavioral categories:

Comfort behavior: Self-directed behaviors such as pecking at the feathers or rubbing the head on the midback, preening, dustbathing, scratching with a foot or bill, stretching, ruffling feathers, and shaking the whole body or a body part.

Aggression: Aggression could be delivered by jabbing the bill directly into another bird, pecking through the pen mesh at a neighbor, jumping toward a neighbor with feet directed forward in a raking position, and bill sparring when one bird stood front to front with another and the other backed down. Both delivering aggression and receiving aggression were recorded.

Foraging: Included behaviors such as eating, drinking, pecking the air, walking with the head and neck directed at the ground, and pecking at inanimate objects.

Non-vigilant: When lying or standing, the neck was relaxed in an 'S' posture, and the eyes were open.

Sleeping: The bird was lying on its belly or side or standing motionless while maintaining the eyes closed.

Vigilant: The bird's neck was extended in a straight line perpendicular to the ground and the bill was parallel to the ground or pointed up. Eyes were open.

Out of view: The focal bird was out of sight of the observer.

Although the frequencies of aggression are not comparable across treatments given our experimental conditions (e.g., confounding from pen size and population density), given the lack of studies in this species, we included them in our observations.

2.5. Statistical analysis

From the observations, the percentage of time that each bird spent performing the behavioral categories per 5-min observation was calculated. If the bird was out of view for part of the observation then percentages were calculated according to the proportion of time that the bird was in full view. For the purposes of analysis, data were broken down into two-week periods from hatching to 20 weeks of age. Two-week age periods were selected because of logistical limitations in the number of observations that could be collected in one week. Because several observations were collected within each two-week period, multiple observations were averaged for each bird at each time of day (am or pm) within each two-week period. The average number of 5-min observations per bird per period per time of day was 3.54 and the average percentage of time out of view was only 0.98%.

Data were analyzed using repeated measures mixed models analysis of variance (ANOVA) with the subject factor being individual birds (SAS, 1996). Factors included in the model were rearing treatment, time of day, and age period as the repeated measure. Year was not included in the ANOVA model because year effects were confounded with individual crane effects. Therefore, data were pooled over the two years of study.

Normality of residuals was tested using the Shapiro–Wilks statistic and Kolmogrov D statistic (Sokal and Rohlf, 1969). Akaike's Information Criterion (SAS, 1996) identified compound symmetry, homogeneous variance structure as the model with the best fit for the variance–covariance structure of the models tested (e.g., compound symmetry, autoregressive). A posteriori mean comparisons were calculated using Tukey's multiple comparison procedure on the least square means.

Pearson correlation coefficients were calculated to compare mean proportions for behaviors among the 34 birds of primary interest that were reintroduced as part of the nonmigratory flock at the release site in Florida (Kreger, 2003; Kreger et al., in review, in preparation). This provides consistency for comparing behavior of the same birds pre- and post-reintroduction. The age of 18–20 weeks old was chosen to calculate correlations because it was the period closest to the age of release, representing the period at which the birds were the most mature, and would avoid confounding effects with earlier developmental changes. The correlations were based on the mean of all observations for each bird for the period of 18–20 weeks for each behavior. Results from these correlations should be interpreted with caution because, as the number of correlations calculated increases, so does the risk of increasing the overall Type I error. Thus, correlations among rearing treatments were not calculated.

3. Results

Regardless of rearing treatment, most of the time the birds (n = 56) were nonvigilant (37.88% \pm 0.73) (arithmetic mean \pm S.E.), foraging (33.40% \pm 0.83), vigilant (13.13% \pm 0.80), or performing comfort behaviors (9.61% \pm 0.49) when compared to other behaviors. Because some behavioral states and activities were low in percentage making their statistical analysis unfeasible, only their means are presented. Behaviors that were

infrequent included receiving aggression (0.05% \pm 0.02), delivering aggression (0.07% \pm 0.02), and sleeping (4.26% \pm 0.44).

ANOVA results for the four most frequent behaviors are presented in Table 1. We inspected all Tukey comparisons for 2-way and 3-way interactions. Although some were significant, there were no differences of biological relevance. For example, some statistically significant interactions such as rearing treatment $(R) \times \text{age}(A) \times \text{time}$ of day (T) are not discussed when significant effects were among R at different A rather than among R with the same A. All other significant interactions are discussed below.

The interaction of $R \times T$ for comfort behaviors (Table 1) indicated that HR and HRE birds spent more time than PR (Fig. 1a) doing this behavior in the pm than in the am. For all rearing treatments, birds spent more time performing comfort behaviors from four to eight weeks of age in the pm than in the am $(T \times A, \text{Table 1}, \text{Fig. 1b})$. The time of day differences decreased as morning comfort behavior increased and afternoon comfort behaviors decreased from 10 weeks of age onward (Fig. 1b).

In general, the percentage of time invested in foraging activities was significantly higher from 4 to 6 weeks of age during the am, than from 6 weeks onward ($T \times A$, Table 1, Fig. 2a). At this age, differences for time of day disappeared as the percentage of time spent foraging increased in the afternoon. Foraging did not differ among rearing treatments until 18–20 weeks of age when PR birds showed significantly less foraging behavior than HRE birds ($R \times A$, Table 1, Fig. 2b).

Regarding vigilance and nonvigilance behaviors, the significant interaction of $R \times T$ indicated that the percentage of time spent nonvigilant for PR and HR birds was greater in the pm than in the am (Table 1, Fig. 3). As with other behaviors, there were no significant differences between HR and HRE birds. In general, PR birds were more vigilant than HR and HRE birds throughout rearing ($R \times A$, Table 1). However, the differences across these treatments also depended on the age of the birds and the time of day ($R \times T \times A$, Table 1). In the morning (Fig. 4a) PR birds spent significantly more time vigilant than HR and HRE birds from 6–16 weeks of age, and in the afternoon (Fig. 4b) PR birds spent significantly more time vigilant than HR and HRE birds from 14–20 weeks of age.

Pearson correlations conducted on the final age period before quarantine (18–20 weeks of age) of the 34 birds used for reintroduction indicated that several behaviors were significantly associated. An inverse correlation was found between percentage of time foraging and vigilance (r = -0.686, P < 0.0001). The percentage of time foraging was also negatively correlated to the percentage of time nonvigilant (r = -0.481, P = 0.0040). These correlations, however, may be due to the fact that percentages add to 100%, so some such correlations are expected with this type of data collection methodology.

4. Discussion

The objective of this study was to determine the extent that management practices of hand rearing and parent rearing affected the behavior of young whooping cranes. This work consistently showed no differences in the behavior of birds reared under HR or HRE management practices. The only difference in the management between HR and HRE birds was that HRE birds were taken on supplemental short walks once a day for the first 25 days.

Table 1 Summary statistics (F-values, P-values, and degrees of freedom) from the repeated measures analysis of variance (ANOVA) of the behavioral percentages for n = 56captive-bred whooping cranes (Grus americana) from 0-20 weeks of age

	Fixed effects terms in ANOVA model													
d.f.	Time ^b		Age ^c		Time × Age		Rearing treatment ^d		Rearing × Time		Rearing × Age		Rearing × Time × Age	
	1	53	9	426	9	423	2	53	2	53	18	426	18	423
Behavior ^a	F	P	\boldsymbol{F}	P	F	P	F	P	\boldsymbol{F}	P	F	P	F	P
Comfort	7.86	0.0070	5.62	< 0.0001	3.24	0.0008	4.93	0.0109	4.83	0.0118	1.89	0.0151	0.49	0.9624
Forage	28.28	< 0.0001	15.12	< 0.0001	2.58	0.0068	6.87	0.0022	0.43	0.6534	1.50	0.0870	1.04	0.4096
Non-vigilance	53.79	< 0.0001	9.93	< 0.0001	0.56	0.8300	0.05	0.9521	3.90	0.0262	2.57	0.0004	1.86	0.0172
Vigilance	8.24	0.0059	17.71	< 0.0001	1.86	0.0560	32.97	< 0.0001	1.58	0.2150	2.22	0.0030	1.83	0.0199

See text for descriptions of the behaviors and for details concerning the ANOVA models.

^a Percentage of time spent performing the behavior per 5-min observation period.

^b Time of day during observation period (either morning, 0500–0800, or afternoon, 1530–1830).

^c Age of individual during observation (10 2-week intervals from 0–20 weeks of age).

d Rearing treatment (parent reared, hand reared, or hand reared with exercise).

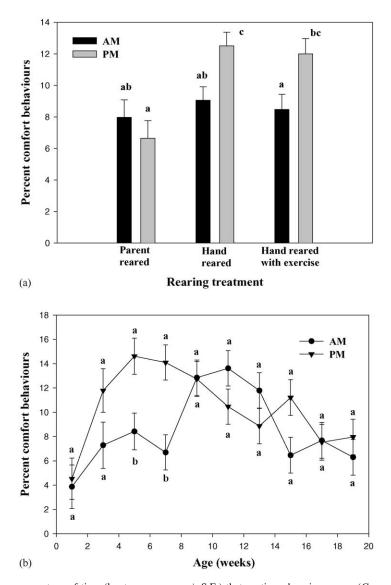


Fig. 1. Mean percentage of time (least square mean \pm S.E.) that captive whooping cranes (*Grus americana*) engaged in comfort behavior for (a) the three rearing treatments in the am and pm periods, averaged over 0–20 weeks of age, and (b) the different time periods from 0–20 weeks of age, averaged over rearing treatment. Means which share the same letter are not significantly different (Tukey pairwise comparisons, P > 0.05). Comparisons in (b) are made only between time of day within each age period.

Following this period both groups were treated identically. Thus, the addition of a short period of extra exercise to the HRE birds did not seem to have an impact on their behavior. Although we did not directly collect information on leg problems, its incidence was rare in either HR or HRE birds. Therefore, since no differences in behavior or leg problems were

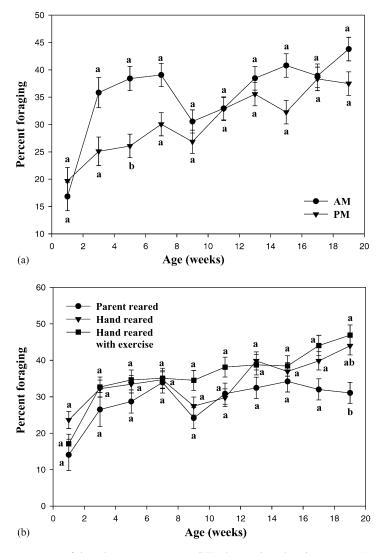


Fig. 2. Mean percentage of time (least square mean \pm S.E.) that captive whooping cranes (*Grus americana*) engaged in foraging behavior according to (a) time of day, averaged over rearing treatment, and (b) for the three rearing treatments from 0–20 weeks of age, averaged over time of day. Means which share the same letter are not significantly different within each age period (Tukey pairwise comparisons, P > 0.05).

noted in this experiment, our results suggest that the additional effort in handling of the HRE birds to provide them with the extra exercise does not modify the time spent performing the behaviors measured.

PR birds differed from HR and HRE in the amount of time engaged in comfort behaviors and vigilance. PR birds showed significantly lower levels of comfort behavior than HR and HRE birds in the afternoon, but no differences in the morning. This difference probably is due to the fact that birds in the HR and HRE treatments were allowed to swim

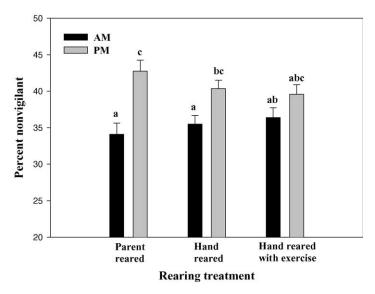


Fig. 3. Mean percentage of time (least square mean \pm S.E.) that captive whooping cranes (*Grus americana*) engaged in nonvigilant behavior for the three rearing treatments during the am and pm periods, averaged over 0–20 weeks of age. Means which share the same letter are not significantly different (Tukey pairwise comparisons, P > 0.05).

daily and walked to a small marsh in the afternoon. It is expected that wet plumage would trigger much more preening and other comfort behaviors. Thus, higher pm levels of comfort behaviors occurred from 4 to 8 weeks of age when HR and HRE birds were housed in individual pens but taken on walks to the marsh. After 8 weeks, when the birds were placed in social groups, they were no longer walked to marshy areas and there were no differences among rearing treatments or time of day.

Whooping crane young spent 13.1% of the time engaged in vigilant behavior, which is remarkably similar to the mean 14.4% vigilance levels observed through the day in wild adult and juvenile sandhill cranes (Sparling and Krapu, 1994). However, PR birds spent more time being vigilant than HR and HRE birds throughout the day and for most of the rearing period. This finding is contrary to Horwich (2001) who, based on his experience but not tested data, suggested that PR crane young must not be as vigilant as HR crane young in captivity because the parents provide heightened vigilance. This study demonstrated that birds reared with adults were often observed to be more vigilant than HR and HRE birds. Similar results were found in studies comparing vigilance levels in PR and HR captive grey partridges (*Perdix perdix*) (Beani and Dessì-Fulgheri, 1998) and common ravens (*Corvus corax*) (Valutis and Marzluff, 1999).

The social environment may have affected the rearing treatment differences in vigilance. PR young may have imitated adult vigilant behavior from observing the parents. PR adult birds were observed responding with alarm calls when vehicles drove outside the pen compound, when raptors soared above the pens, or when a caretaker came within visual range (Kreger, pers. obs.). The adult birds adopting a vigilant posture and standing still accompanied these vocalizations. The young immediately adopted the same posture

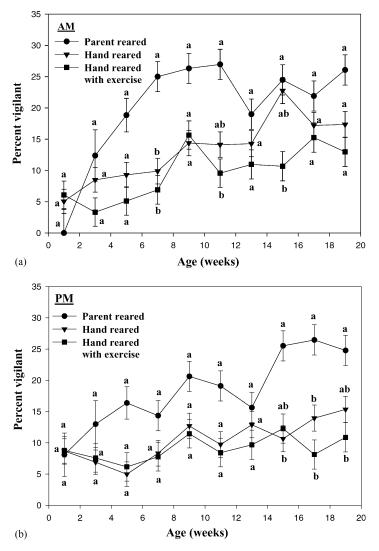


Fig. 4. Mean percentage of time (least square mean \pm S.E.) that captive whooping cranes (*Grus americana*) engaged in vigilant behavior during the (a) am and (b) pm time periods for the three rearing treatments from 0–20 weeks of age. Means which share the same letter are not significantly different within each age period (Tukey pairwise comparisons, P > 0.05).

although they were unable to emit the same vocalizations (Kreger, pers. obs.). Thus, the young may have learned to be more vigilant from observing the parents. This is not surprising as, depending on the bird species, young may learn predator recognition, nestbuilding skills, offspring rearing, migratory routes, and appropriate vocalizations from parents during critical stages in their development (Alonso and Alonso, 1993; Curio, 1998; Hutchins et al., 1995).

In contrast to the greater percentage of vigilance observed in PR birds, two factors may have contributed to the lower levels of vigilance in HR and HRE birds: the interactions with costumed humans, and/or lack of social interactions with a sub-adult crane or with sameage conspecifics. HR and HRE birds interacted frequently with humans. The costume worn by caretakers was designed to mimic the physical appearance of adult cranes. Costumed caretakers, however, did not pause in their activities to adopt vigilant postures. Even if caretakers were to include vigilant postures when working around the young, the young may just fail to recognize the behavior. Although it is unknown when a crane should be vigilant and for how long, what appears to be a lack of adequate vigilant behavior levels in HR and HRE birds may have implications for their chances of survival. It has been demonstrated that failure to be vigilant at the appropriate time in the wild may result in predation or competitive disadvantages (e.g., territory loss) (Curio, 1998) or higher predation (Van Heezik and Seddon, 1998; Miller et al., 1990).

Interactions with humans may also have produced a taming effect on HR and HRE birds; thus costumed humans were not viewed as predators. Tameness is defined as the absence of fear and aggressive responses towards humans and tolerance to handling (Aengus and Millam, 1999). Early handling of many captive species has been shown to increase exploratory behavior and reduce the animal's fear of novel objects and human approaches (Levine et al., 1967; Anderson et al., 1972; Hemsworth et al., 1986; Pedersen and Jeppesen, 1990). HR and HRE birds were imprinted on costumed caretakers and the chicks were handled frequently when the birds were taken on daily walks, placed in a swimming pool during supervised swimming sessions, and weighed. Because there was more neonatal handling of HR and HRE whooping crane chicks by people than PR chicks, HR and HRE birds were likely to be tamer and this may have affected the expression of vigilant behavior. Even simple exposure to visitors and environmental noises from caretaker activity tend to produce lower flight distances from caretakers in captive-bred zoo animals (Hediger, 1964; Carlstead, 1996).

Although vigilance may have a genetic component, animals may improve their responses to predators through experience (Miller et al., 1990; Griffin et al., 2000) by observing the actions of another conspecific or the group when faced with a predatory threat (Curio, 1993; McLean et al., 1999). Thus, HR and HRE birds in social groups may not have spent as much time engaged in vigilance as PR birds of the same age because they did not recognize potential predators or were not exposed to experienced birds enough to teach them how to react.

Lastly, although HR and HRE young were within the visual and auditory range of a sub-adult live crane, the model may have not been sufficient to influence vigilant behavior as much as breeding pairs that raise young. This lack of effect could be due to the fact that there were fewer live models than the number of adults in the PR yards or could be related to the lack of direct social interaction between the sub-adults and the young. This experiment therefore suggests that simple visual exposure to the adult model may not have any detectable effect to the behavior of the young.

We note that there was an inverse correlation between vigilance and foraging. While this may be a result of our data collection methodology (i.e., percentages add to 100%), it likely supports previous indications that animals must balance foraging and vigilance to minimize predation and maximize fitness (Pulliam, 1973; Quenette, 1990; Cuthill and

Houston, 1997). Thus, regardless of rearing treatment, all birds demonstrated some level of alertness and may have alternated bouts of foraging with bouts of vigilance. The optimal level of vigilance and foraging in wild birds depends on such factors as group size, predator pressure, and habitat characteristics.

The crane chicks tended to forage more in the morning until the tenth week when levels of foraging between morning and afternoon were similar. Although the birds always had 24-h access to food in feeders, this more evenly distributed foraging behavior throughout the day may be due to their growth. As they grew and became physically more mobile the birds were better able to coordinate probing and scanning activities to hunt for invertebrates throughout the day that supplemented their diet. In the PR birds, such mobility was observed as the young matured and spent more time following the parents and pecking at the ground whenever the adult stopped to feed. Caretakers, through walks, encouraged increased mobility of HR and HRE birds.

In summary, this study demonstrated that the behavior of captive-reared juvenile whooping cranes is to some extent affected by rearing treatment. There were also differences in their behavior that were associated with age and time of day. Main behavioral differences among rearing treatments were that PR birds spent more time being vigilant than HR and HRE birds throughout rearing. The percentages of time engaged in foraging and vigilance across rearing treatments suggests some level of wariness among foraging birds to reduce predation or competition risk.

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References

Aengus, W.L., Millam, J.R., 1999. Taming parent-reared orange-winged Amazon parrots by neonatal handling. Zoo Biol. 18, 177–187.

Allen, R.P., 1952. The whooping crane. Nat. Audubon Soc. Res. Report 3, 246.

Alonso, J.A., Alonso, J.C., 1993. Age-related differences in time budgets and parental care in wintering common cranes. The Auk 110, 78–88.

Anderson, C.O., Denenberg, V.H., Zarrow, M.X., 1972. Effects of handling and social isolation upon the rabbit's behaviour. Behaviour 43, 165–175.

Archibald, G.W., Lewis, J.C., 1996. Crane biology. In: Ellis, D.H., Gee, G.F., Mirande, C.M. (Eds.), Cranes: Their Biology, Husbandry, and Conservation. Hancock House Publishers, Blaine, Washington, pp. 1–30.

Ballou, J.D., Foose, T.J., 1996. Demographic and genetic management of captive populations. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, pp. 263–283.

- Beani, L., Dessì-Fulgheri, F., 1998. Anti-predator behaviour of captive Grey partridges (*Perdix perdix*). Ethol. Ecol. Evol. 10, 185–196.
- Carlstead, K., 1996. Effects of captivity on the behavior of wild mammals. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, pp. 317–333.
- Castro, M.I., Beck, B.B., Kleiman, D.G., Ruiz-Miranda, C.R., Rosenberger, A.L., 1998. Environmental enrichment in a reintroduction program for golden lion tamarins (*Leontopithecus rosalia*). In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.), Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press, Washington, D.C. and London, United Kingdom, pp. 113–128.
- Clutton-Brock, 1991. The Evolution of Parental Care. Princeton University Press, New Jersey.
- Crockett, C.M., 1996. Data collection in the zoo setting, emphasizing behavior. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, pp. 545–565.
- Curio, E., 1993. Proximate and developmental aspects of antipredator behavior. Adv. Study Behav. 22, 135–238.
 Curio, E., 1998. Behavior as a tool for management intervention in birds. In: Caro, T. (Ed.), Behavioral Ecology and Conservation Biology. Oxford University Press, New York, pp. 164–187.
- Cuthill, I.C., Houston, A.I., 1997. Managing time and energy. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioural Ecology: An Evolutionary Approach. Blackwell Science, Oxford, pp. 97–120.
- Ellis, D.H., Archibald, G.W., Swengel, S.R., Kepler, C.B., 1991. Compendium of crane behavior. Part 1: Individual (nonsocial) behavior. Proc. North Am. Crane Workshop, International Crane Foundation, Baraboo, Wisconsin 5, 225–234.
- Ellis, D.H., Lewis, J.C., Gee, G.F., Smith, D.G., 1992. Population recovery of the whooping crane with emphasis on reintroduction efforts: past and future. Proc. North Am. Crane Workshop, International Crane Foundation, Baraboo, Wisconsin 6, 142–150.
- Ellis, D.H., Swengel, S.R., Archibald, G.W., Kepler, C.B., 1998. A sociogram for the cranes of the world. Behav. Process. 43, 125–151.
- Ellis, D.H., Gee, G.F., Hereford, S.G., Olsen, G.H., Chisolm, T.D., Nicolich, J.M., Sullivan, K.A., Thomas, N.J., Nagendran, M., Hatfield, J.S., 2000. Post-release survival of hand-reared Mississippi sandhill cranes. The Condor. 102, 104–112.
- Gee, G.F., 1983. Crane reproductive physiology and conservation. Zoo Biol. 2, 199-213.
- Gee, G.F., Mirande, C.M., 1996. Artificial insemination. In: Ellis, D.H., Gee, G.F., Mirande, C.M. (Eds.), Cranes: Their Biology, Husbandry, and Conservation. Hancock House Publishers, Blaine, Washington, pp. 205–218.
- Griffin, A.S., Blumstein, D.T., Evans, C.S., 2000. Training captive-bred or translocated animals to avoid predators. Conserv. Biol. 14, 1317–1326.
- Hediger, H., 1964. Wild Animals in Captivity. Dover Publications, New York.
- Hemsworth, P.H., Barnett, J.L., Hansen, C., Gonyou, H.W., 1986. The influence of early contact with humans on subsequent behavioral response of pigs to humans. Appl. Anim. Behav. Sci. 15, 55–63.
- Horwich, R.H., 1996. Imprinting, attachment, and behavioral development in cranes. In: Ellis, D.H., Gee, G.F., Mirande, C.M. (Eds.), Cranes: Their Biology, Husbandry, and Conservation. Hancock House Publishers, Blaine, Washington, pp. 117–119.
- Horwich, R.H., 2001. Developing a migratory whooping crane flock. North Am. Crane Workshop 8, 85-95.
- Hutchins, M., Sheppard, C., Lyles, A.M., Casedi, G., 1995. Behavioral considerations in the captive management, propagation, and reintroduction of endangered birds. In: Gibbons, E.F., Durrant, B.S., Demarest, J. (Eds.), Conservation of Endangered Species in Captivity: An Interdisciplinary Approach. State University of New York Press, Albany, NY, pp. 263–289.
- Kleiman, D.G., 1996. Reintroduction programs. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, pp. 297–305.
- Költringer, C., Sodeikat, G., Curio, E., 1995. Antipredator behavior of the black grouse *Tetrao tetrix* chicks as influenced by hen-rearing versus hand-rearing. In: Jenkins, D. (Ed.), Proc. Intern. Symp. Grouse 6: World Pheasant Association, Reading, UK; and Istituto Nazionale 1993 per la Fauna Selvatica, Ozzano dell'Emelia, Italy, 81–83.

- Kreger, M.D., 2003. Behavioral Profiles of the Captive Juvenile Whooping Crane (*Grus americana*) as an Indicator of Reintroduction Behavior and Survival. Doctoral Dissertation. University of Maryland, College Park, Maryland, 241.
- Kreger, M.D., Hatfield, J.S., Estevez, I., Gee, G.F., Clugston, D.A., in review. The effects of captive rearing on behavior of newly-reintroduced whooping cranes (*Grus americana*). Submitted to J. Appl. Anim. Behav. Sci.
- Kreger, M.D., Hatfield, J.S., Estevez, I., Gee, G.F., Clugston, D.A., in preparation. Behavioral profiles of the captive juvenile whooping crane (*Grus americana*) as an indicator of post-release survival.
- Kreger, M.D., Hutchins, M., Fascione, N., 1998. Context, ethics, and environmental enrichment in zoos and aquariums. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.), Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press, Washington, DC and London, United Kingdom, pp. 59–82.
- Lehner, P.N., 1996. Handbook of Ethological Methods, second ed. Cambridge University Press, New York.
- Levine, S., Haltmeyer, G.C., Karas, G.G., Denenberg, V.H., 1967. Physiological and behavioral effects of infantile stimulation. Physiol. Behav. 2, 55–59.
- Martin, P.R., Bateson, P., 1993. Measuring Behaviour: An Introductory Guide, second ed. Cambridge University Press, Cambridge and New York.
- McLean, I.G., Hölzer, C., Strudholme, B.J.S., 1999. Teaching predator recognition to a native bird: implications for management. Biol. Conserv. 87, 123–130.
- Miller, B., Biggins, D., Wemmer, C., Powell, R., Calvo, L., Hanebury, L., Wharton, T., 1990. Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*): II. Predator avoidance. J. Ethol. 8, 95– 104.
- Nesbitt, S.A., Folk, M.J., Sullivan, K.A., Schwikert, S.T., Spalding, M.G., 2001. An update of the Florida whooping crane release project through June 2000. Proc. North Am. Crane Workshop 8, 62–72.
- Olsen, G.H., 1994. Orthopedics in cranes: pediatrics and adults. Semin. Avian Exotic Pet Med. 3 (2), 73-80.
- O'Malley, K., 1999. Protocol for Hand-rearing Crane Chicks–1999. Unpublished, Patuxent Wildlife Research Center, Laurel, Maryland, 33.
- Pedersen, V., Jeppesen, L.L., 1990. Effects of early handling on later behaviour and stress responses in the silver fox (Vulpes vulpes). Appl. Anim. Behav. Sci. 26, 383–393.
- Powell, A.N., Cuthbert, F.J., 1993. Augmenting small populations of plovers: an assessment of cross-fostering and captive-rearing. Conserv. Biol. 7, 160–168.
- Pulliam, H.R., 1973. On the advantages of flocking. J. Theor. Biol. 95, 89-103.
- Quenette, P.Y., 1990. Functions of vigilance in mammals: a review. Acta Ecologica. 11, 801-818.
- SAS, 1996. Statistical Analysis System, Version 6.12. SAS Institute, Cary, North Carolina.
- Snyder, N., Derrickson, S., Bessinger, S.R., Willey, J.W., Smith, T.B., Toone, W.D., Miller, B., 1996. Limitations of captive breeding in endangered species recovery. Conserv. Biol. 10, 338–348.
- Sokal, R.R., Rohlf, F.J., 1969. Biometry. W.H. Freeman and Co, San Francisco, California.
- Sparling, D.W., Krapu, G.L., 1994. Communal roosting and foraging behavior of staging sandhill cranes. Wilson Bull. 106, 62–77.
- Swengel, S.R., Archibald, G.W., Ellis, D.H., Smith, D.W., 1996. Behavior management. In: Ellis, D.H., Gee, G.F., Mirande, C.M. (Eds.), Cranes: Their Biology, Husbandry, and Conservation. Hancock House Publishers, Blaine, Washington, pp. 105–122.
- Swengel, S.R., Carpenter, J.W., 1996. General husbandry. Hancock House Publishers, Blaine, Washington.
- U.S. Fish and Wildlife Service, 1994. Whooping Crane Recovery Plan. Albuquerque, New Mexico, 92.
- Valutis, L.L., Marzluff, J.M., 1999. The appropriateness of puppet-rearing birds for reintroduction. Conserv. Biol. 13, 584–591
- Van Heezik, Y., Seddon, P.J., 1998. Ontogeny of behavior of hand-reared and hen-reared captive houbara bustards. Zoo Biol. 17, 245–255.
- Van Heezik, Y., Seddon, P.J., Maloney, R.F., 1999. Helping reintroduced houbara bustards avoid predation: effective anti-predator training and the predictive value of pre-release behavior. Anim. Conserv. 2, 155–163.
- Vargas, A., Anderson, S.H., 1999. Effects of experience and cage enrichment on predatory skills of black-footed ferrets (*Mustela nigripes*). J. Mammal. 80, 263–269.
- Wallace, M.P., 1994. Control of behavioral development in the context of reintroduction programs for birds. Zoo Biol. 13, 491–499.

- Wassmer, D.A., Guenther, D.D., Layne, J.N., 1988. Ecology of the bobcat in south-central Florida. Bull. Florida State Mus. Biol. Sci. 33, 159–228.
- Watanabe, T., 1996. Comparison of Behavioral Ontogeny and Ethology of Whooping Crane and Greater Sandhill Crane Chicks, Masters Thesis, Southern Connecticut State University, New Haven, Connecticut, 130.
- Weller, M.W., Ward, P., 1959. Migration and mortality of hand-reared redheads (Aythya americana). J. Wildl. Manage. 23, 427–433.
- Wellington, M., Burke, A., Nicolich, J.M., O'Malley, K., 1996. Chick rearing. In: Ellis, D.H., Gee, G.F., Mirande, C.M. (Eds.), Cranes: Their Biology, Husbandry, and Conservation. Hancock House Publishers, Blaine, Washington, pp. 77–94.